

VOCAL INTERACTION BETWEEN TWO MALE GIBBONS, *HYLOBATES LAR*

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ABSTRACT

Male lar gibbons (*Hylobates lar*) produce long solo bouts of loud calls. These calls are thought to function at a distance in mate attraction and/or territorial rivalry. We present evidence that two subadult males, who were not neighbours and could seldom see one another, interacted through these solos. We suggest that they interacted because they were rivals, who lacked a common border at which to test each other by chasing and fighting, and who therefore resorted to matching their daily call durations as a means of augmenting the assessment value of their calls.

INTRODUCTION

Gibbons are monogamous, territorial, tree-living apes of Southeast Asia. They are noted for their calls, which are loud, long and complex and which, in different species, comprise different combinations of solos and/or duets by bonded pairs (MARSHALL & MARSHALL, 1976; HAIMOFF, in press). It is reasonable to suppose that these loud calls function in communication between groups, whether or not they also carry a within-group function.

One possible manifestation of such communication is vocal duelling. Routine border disputes between groups, involving chases, include more or less specialised calls in most gibbon species. Groups facing each other across a border may also exchange duets, which are not specialised for disputes. In these cases groups may or may not chase as well (see BROCKELMAN & SRIKOSAMATARA, 1984, for a review of intergroup relations in gibbons). But are the daily duets and solos delivered from well inside the territory, out of sight of other groups, used in vocal duelling at a distance?

TENAZA (1976) suggests that a form of vocal duelling, countersinging, occurs regularly in Kloss' gibbon (*Hylobates klossii*). Females delivering concurrent solos are said to countersing by deliberately overlapping phrases, while males in the same circumstance are said to countersing by deliberately alternating phrases. As stressed by WHITTEN (1982), however, countersinging has not yet been demonstrated statistically in gibbons. This is largely due to the problems of interdependence of data points and inflated sample sizes which arise in such analyses.

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One way of demonstrating countersinging which avoids these problems is to show matching changes of phrase delivery rate by two animals calling concurrently (as ROSEN & LEMON, 1974, did for an anuran). We found no sign of this in an analysis of solos by male lar gibbons (*H. lar*) (unpublished observations). However, we present evidence of vocal duelling using another approach, testing the daily calling durations of two subadult male gibbons to see whether they matched, and comparing them with a range of controls.

MATERIALS AND METHODS

The results reported here are drawn from a study of the vocal behaviour of lar gibbons (*Hylobates lar entelloides*) in Khao Yai National Park, Thailand (101°22'E, 14°26'N, 130 km NE of Bangkok). The study site lies on the hill just west of park headquarters, deep inside the park's 2000 km² of continuous forest. The site measures 1.5 km × 2 km and is covered by evergreen rain forest. There is a marked dry season about December-March and a wet season about April-November, with some variation in timing between years. Annual rainfall on site is likely to be well in excess of the 1500 mm recorded in a rain gauge placed in a small canopy gap created by a tree-fall. The terrain consists of steep ridges and gullies, and altitude ranges from 730 m to 870 m above sea level. The site is interspersed with old fields in various stages of regrowth, not entered by gibbons.

The study population comprises territorial, monogamous social groups of gibbons, with one to four offspring per group (Fig. 1). We are concerned here with the solo call bouts of two subadult males, Gormless in group G and Fearless in group F. Subadult males are fully grown but not yet mated, and still live in their parents' territories, from which they give solo call bouts. Fearless and Gormless were the only two subadult males who called for periods of several months during our study. Fearless was already calling when we arrived in January 1981, and continued until after we had left in October 1982. Gormless began to call in July 1981; he disappeared in March 1982, presumably in search of a territory of his own. Gormless and Fearless were not neighbours, and during nearly all their solos would have been invisible to each other. However, they did once or twice call from opposite edges of the clearing which separated them, and could then have seen one another.

Solo call bouts are audible for up to 1 km or more through the forest, a distance exceeding the average distance between gibbons in adjacent territories. Gormless and Fearless would usually have been audible to each other. A solo develops quickly from its start into a series of male quaver phrases (Fig. 2), each lasting about 5 s, and delivered at a rate of some 2.5 phrases/min. Solos are given from night trees before

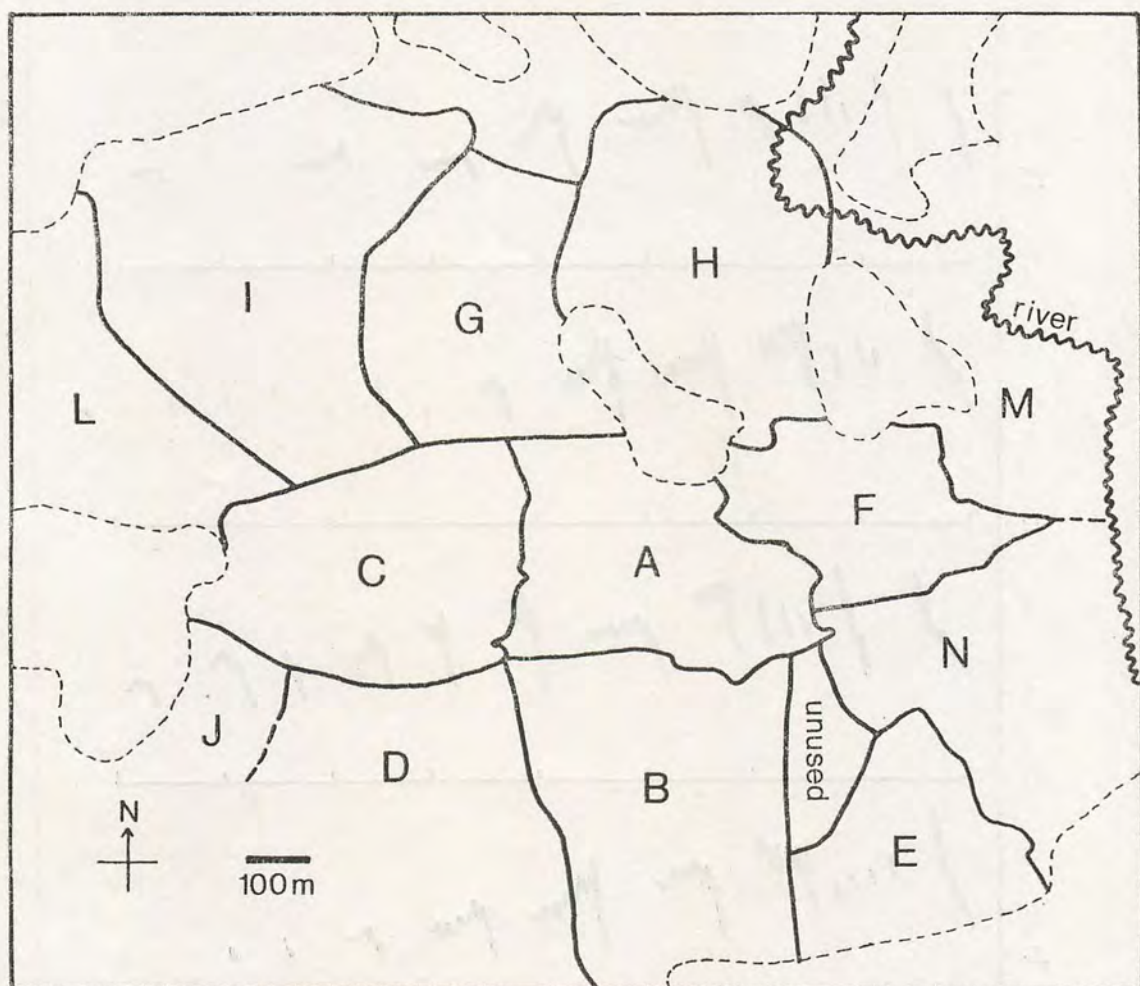


Figure 1. Map of study site, showing territories of gibbon groups. Heavy solid lines mark territory boundaries; fine broken lines mark clearing edges.

or at dawn, or later in the morning from anywhere in the territory (start times peak between 0530 h and 0600 h). They are given by both adult and subadult males; subadults give them more often (1.0 bouts/day compared with 0.2), and their bouts are on average longer (45 min compared with 24 min; RAEMAEKERS, RAEMAEKERS & HAIMOFF, *in press*). A bout is defined as a period of calling separated from other such periods by the same individual by at least 10 min.

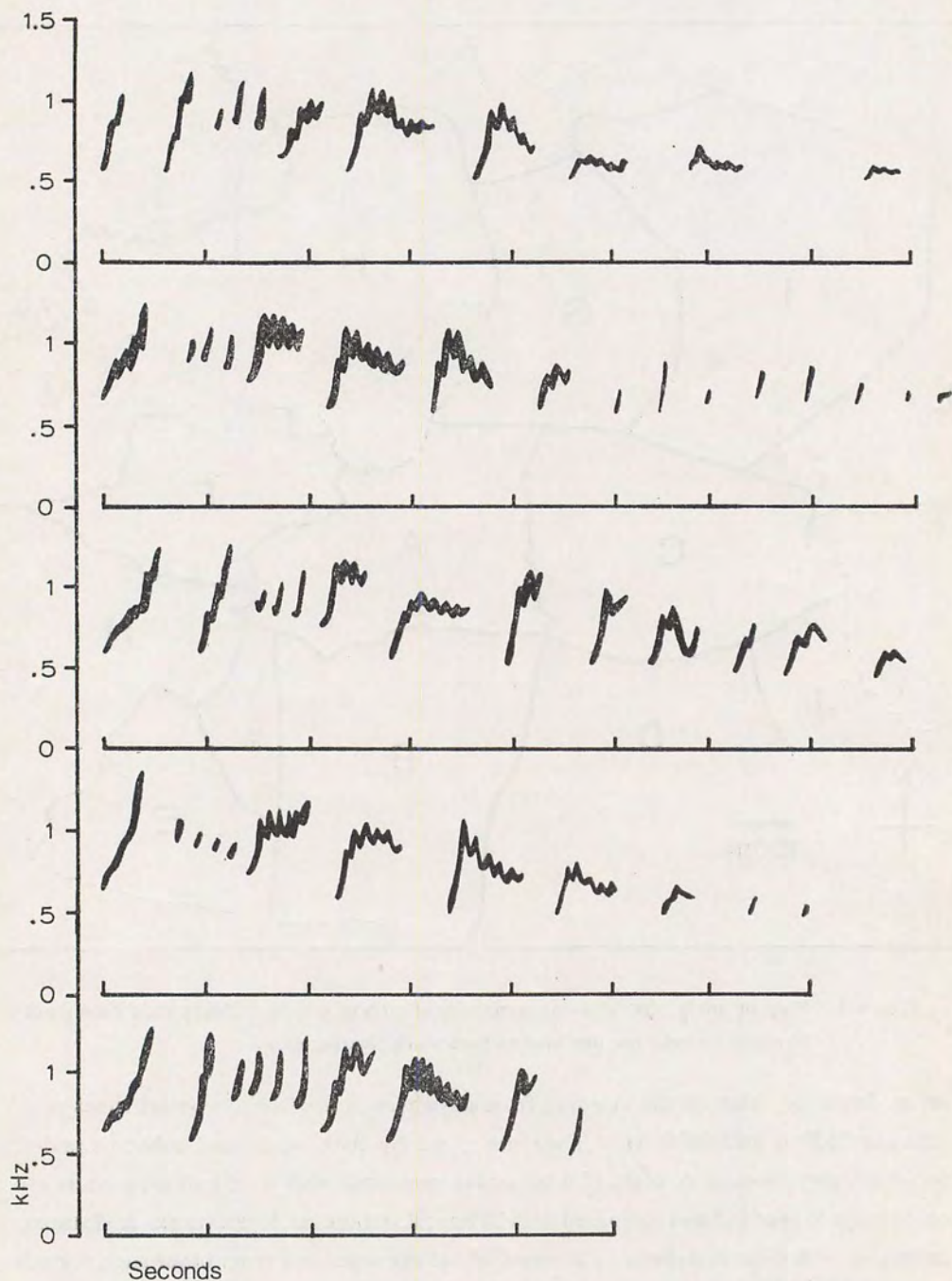


Figure 2. Examples of male quaver phrases produced by Fearless. Tracings of narrow band-pass sonograms.

RESULTS

Daily Call Durations

Daily call duration was measured on those days when both subadults called and we had complete records of the start and stop times of the bouts of each individual. Call duration varied greatly between days (Fearless $X = 66$ min, $SD = 56.4$, $N = 11$. Gormless $X = 66$ min, $SD = 32.6$, $N = 11$). Even so, the two gibbons' daily call durations were closely correlated (Fig. 3) (Spearman $r_s = +0.86$, $N = 11$, $P < 0.01$).

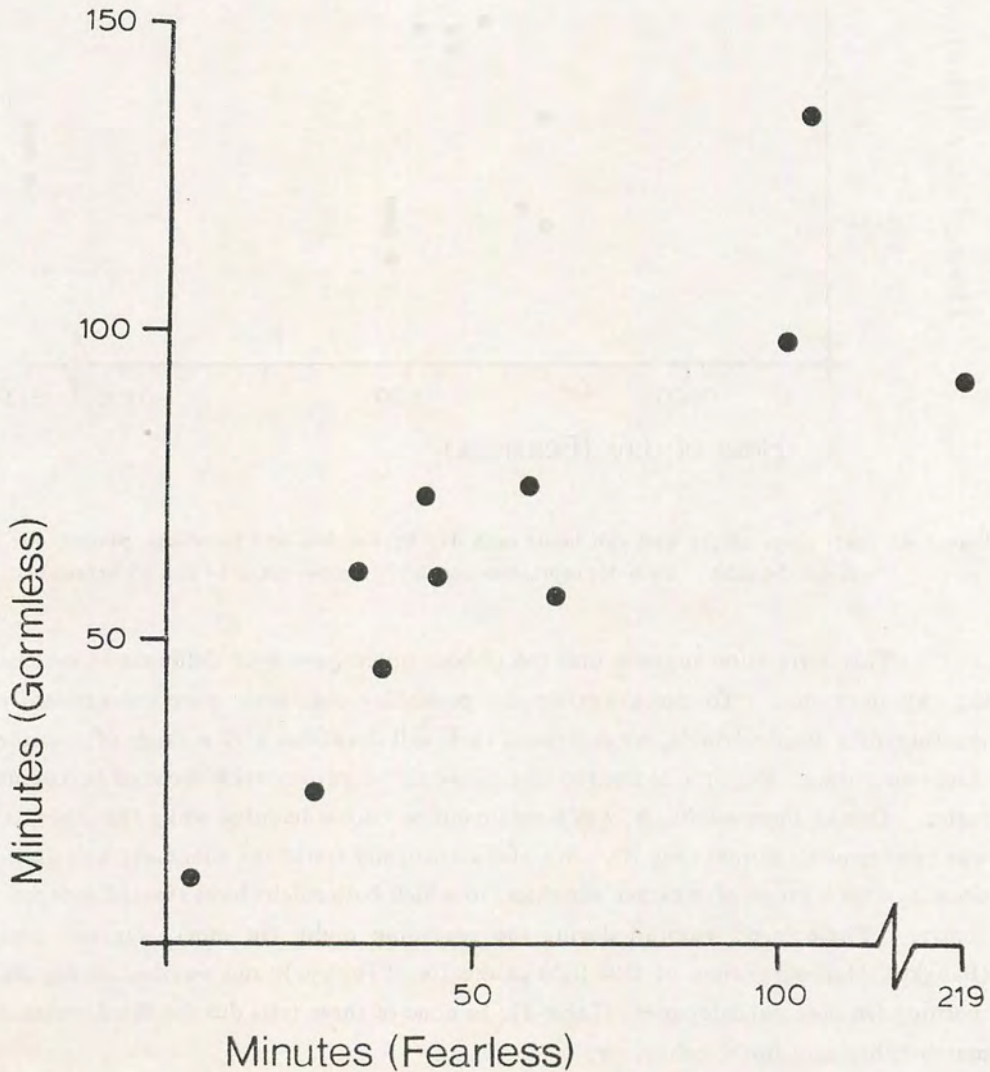


Figure 3. Daily solo calling durations of Fearless and Gormless, plotted one against the other. Each dot represents one day.

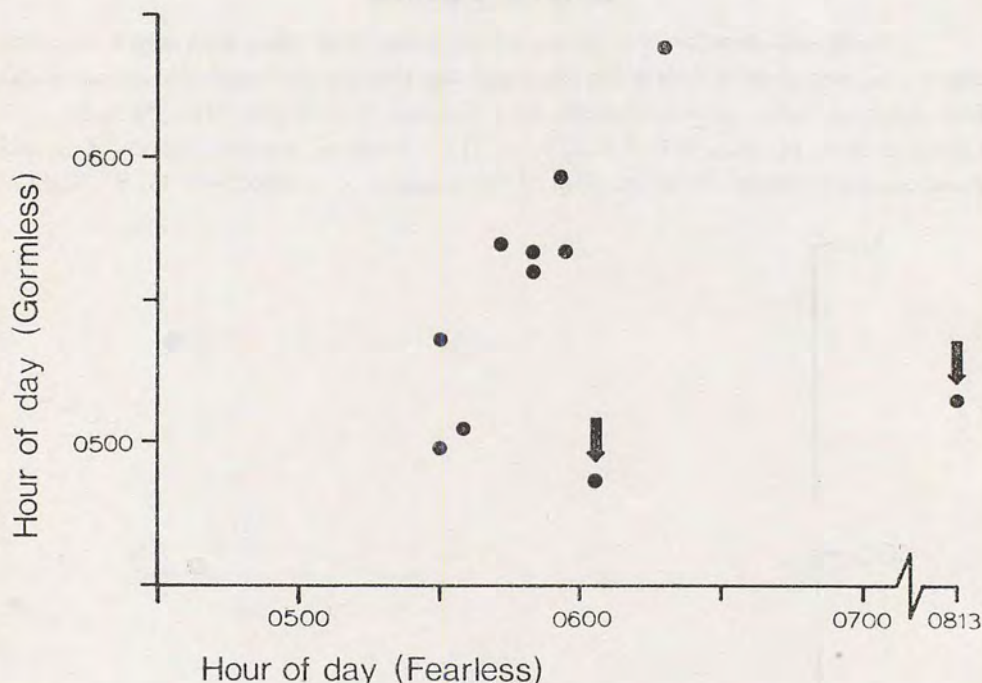


Figure 4. Start times of the first call bouts each day by Fearless and Gormless, plotted one against the other. Each dot represents one day. Arrows mark 14 and 15 September.

This correlation suggests that the gibbons might have been deliberately matching call durations. To check against the possibility that both were independently reacting to a third variable, we compared their call durations with a range of possible third variables. We first compared the subadults' durations with those of two adult males. One of these adults, A, was a neighbour to both subadults, while the other, B, was neighbour to neither (Fig. 1). We also statistically tested the subadults' call durations against a range of weather variables, to which both might have reacted independently. These are: rainfall during the preceding night (in mm); sunrise time (Bangkok Harbour); time of first light in the forest (by eye); and weather during the morning (in nominal categories) (Table 1). In none of these tests did the third variable match either subadult's behaviour.

Table 1. Daily call durations of Fearless and Gormless in 1981, compared with those of A and B adult males and with sunrise and weather data.

Date	Call duration (min)				Sunrise (hr)	First light in forest (hr)	Overnight rain (mm)	Morning weather
	Fearless	Gormless	A adult	B adult				
14 July	44	60	5	0	0554	0530	0	dry, calm, light overcast
17 „	31	61	0	0	0555	?	0	dry, light breeze, sunny
22 Aug	59	75	0	40	0604	0535	6	dry, light breeze, cloudy to light overcast later
23 „	64	57	0	0	0605	?	34	dry, light breeze, sunny
25 „	105	135	0	25	0605	?	9	dry, light breeze, sunny
27 „	42	73	29	0	0605	0535	22	dry, calm to breezy, cloudy to sunny later
14 Sept	4	11	0	0	0607	0539	0	rain at dawn to dry later, calm, cloudy
15 „	101	98	42	25	0607	?	14	dry, calm, light overcast
23 „	35	45	0	29	0608	?	13	rain at dawn to dry later, breezy, cloudy
26 „	24	25	0	17	0608	0535	1	dry, calm to light breeze later, sunny
17 Oct	219	92	30	0	0608	0545	0	dry, light breeze, cloudy

Start Times of Call Bouts

One might expect that, in order to match call durations, the gibbons would have to begin calling fairly close together in time. Fearless began after Gormless on all days but one, when he began in the same minute. The gap between the starts of their first bouts of each day was in fact quite variable (Table 2). Nevertheless, start times did correspond from day to day, except on 14 and 15 September (Fig. 4). For all 11 days, $r_s = +0.25$ (not significant), but when 14 and 15 September are omitted, $r_s = +0.93$ ($P \leq 0.01$). On 14 September Gormless' single bout was short anyway (11 min), and so might not have been very stimulating. On 15 September Gormless gave a very early bout, to which Fearless did not reply, but Fearless did reply one minute after the start of a second bout by Gormless. On balance, the evidence supports the prediction that the subadults' start times would correspond if they were deliberately matching call durations.

Table 2. Start times of the first bouts each day by Gormless and Fearless, and the gap between them.

Date	Start (hrs)		Gap (min)
	Fearless	Gormless	
14 July	0530	0459	31
17 „	0535	0503	32
22 Aug	0550	0536	14
23 „	0648	0623	25
25 „	0557	0540	17
27 „	0556	0556	0
14 Sept	0813	0509	124
15 „	0603	0452	71
23 „	0550	0540	10
26 „	0543	0542	1
17 Oct	0530	0522	8

Long-term Changes in Calling Rate

If Fearless and Gormless deliberately matched call durations, we might expect Fearless to have called more often during the period when Gormless was calling than before or after it. This was so (Table 3, fourth and fifth columns from the left). Fearless called on a higher proportion of days after Gormless had begun (period 1 vs period 2); cut his rate by half after Gormless and gone (period 3 vs period 4, comparing equal samples of days before and after Gormless' last bout); and then returned to a higher rate later on (period 5).

Table 3. Solo calling by Fearless compared with that of Gormless, A adult male, B adult male and season*

Period	Dates	Season	Gormless calling?	Percent days on which called				N (days)
				Fearless	Gormless	A adult	B adult	
1	Apr-June 1981	end of dry, start of wet	no	50	-	15	15	26
2	July-Oct 1981	wet	yes	69	76	27	33	45
3	Jan-March 1982	dry	yes	64	44	4	12	25
4	March-Apr 1982	end of dry, a few showers	no	32	-	8	20	25
5	Apr-Oct 1982	wet	no	58	-	20	35	71

*The gap between periods 2 and 3 is due to the observers' absence.

Table 4. Singing in group H duets by subadult female Hipless. Data divided into the same periods as in Table 3.

Period	No. days on which group H duets noted	No. duets noted	Duets in which Hipless sang	
			No.	%
1. May-June 1981	11	11	1	9
2. July-October 1981	26	26	4	15
3. January-March 1982	7	12	7	58
4. March-April 1982	19	28	26	93
5. April-October 1982	31	35	6	17

It is possible that this was a coincidence. Fearless' changes of rate might have been due to season, or to changes in the rates of surrounding gibbons, which themselves might or might not have been seasonal: calling rates for all classes of bout are lower in dry than wet seasons (RAEMAEKERS, RAEMAEKERS & HAIMOFF, in press). We therefore ran controls, comparing Fearless' rate with season and with the rates of the A and B adult males. Both adults behaved in accordance with a seasonal trend (Table 3). The rise in Fearless' rate in period 2 as compared with period 1 matches those of the adults. However, his rate remained high in period 3 compared with period 2, whereas both adults' rates fell sharply. Moreover, his rate fell by half in period 4 compared with period 3, whereas both adults' rates rose (differences between Fearless and the adults in changes of rate are not quite significant by Fisher's exact test).

Thus, although the initial rise in Fearless' rate after Gormless began could have been a seasonal coincidence, his maintenance of a high rate in period 3 and his sharp drop in rate in period 4 were not seasonal coincidences.

Another possibility is that Gormless and Fearless were independently reacting to the songs of a subadult female in a group which was neighbour to both of them (Hipless in group H). A subadult female almost never sings a solo; her presence is advertised by the great calls she contributes to the duet song bouts of her parents, usually in synchrony with her mother. Hipless' singing in those group H duets we noted is summarised in Table 4. Her frequency of singing is expressed as the percentage of duets in which she sang, rather than the percent of days on which she sang, because we did not hear all group H duets. Comparison of Tables 3 and 4 shows that neither Gormless' nor Fearless' singing rates are well explained by that of Hipless, and are much better explained in terms of each other.

Fearless' return to a higher rate in period 5 could have been purely seasonal, or it could also have been due to the great pressure applied by neighbours to his parents' territory at this time, as his infirm father weakened and his own defence burden increased.

DISCUSSION

The likely function of adult male solos is advertisement of the willingness (GITTINS, 1978) or ability (WHITTEN, 1984) to defend a territory. In keeping with subadults' different status, their solos probably function differently, advertising for a mate, and informing both her and surrounding males of the caller's intention and ability to set up and hold a territory.

We found no evidence of deliberate matching of call durations between adult males, even though it is likely that the solo of one male raises the chances of another male giving a solo. Why should adult and subadult males differ in this respect? Adult males, who hold territories, are probably of interest to each other only if they are neighbours; non-neighbouring adults, buffered by intervening territories, are not a mutual threat. Neighbouring adults can call each other's vocal bluff by chasing and fighting in border disputes. Gormless and Fearless were not neighbours, yet as subadults they would still have been rivals, both for the hand of any local nubile female, and for the place of any local adult male who died or showed exploitable weakness. We suggest that, being unable to test each other's mettle in border disputes, they resorted instead to augmenting the assessment value of their solos by matching their call durations, a behaviour which we may dub 'vocal duelling'. It would be worth checking, in future quantitative studies of gibbon calling, whether this is a general phenomenon.

Both sources of rivalry did exist at the time of these vocal duels: (a) There was a subadult female, Hipless, who was neighbour to both subadult males, and who advertised her presence by calling alongside her mother in parental duets. (b) Fearless' own father, Finn, was in fact weak. Gormless could have sensed this, as we did, through Finn's low calling rate and his lacklustre performance in duets. But Gormless may have been deterred from attempting to replace Finn by the vigorous calling of Fearless, apart from having to cross A's or H's territory on each sortie into F's territory. Fearless took over the burden of territory defence as Finn ailed, and joined Finn in producing the adult male part of the duets with the adult female. Finn died in January 1983 and Fearless replaced him, though he later left to displace the adult male of neighbouring group A in June 1983 (UTHAI TREESUCON, personal communication).

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